COMMENTS ON EASTERN NORTH AMERICAN POLYGYRIDAE

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ABSTRACT

The genitalia and radular structure of several Mesodon *and* Triodopsis *from Arkansas, Oklahoma and West Virginia are illustrated and discussed in relation to their potential significance in phylogenetic studies. The structure of the verge, penial pilaster details, penial sheath muscle attachment, and details of radular cusping are emphasized.*

INTRODUCTION

During a survey of rare and potentially endangered land snail species of Eastern North America, numerous polygyrid land snails were collected. Some of these previously had not been dissected, others were studied in order to check their affinities and compare their structures with those of sympatric taxa. Although the emphasis here is on species from Arkansas and Oklahoma, the opportunity is taken to include information on the West Virginia *Triodopsis (T.) platysayoides* (Brooks, 1933), since its structures differ from those found in *Triodopsis (Neohelix) albolabris alleni* (Wetherby, 1883) and *T. (N.) divesta* (Gould, 1851). The main purpose of this report is to review shell, genital, and radular structures that can be confused on the basis of shell structures and distributional overlap. It is hoped that further work on their ecology and relationships will be stimulated.

The field work by Mr. Glenn Goodfriend was supported by Office of Endangered Species contract 14-16-0008-764, which also paid for the excellent anatomical illustrations by Elizabeth A. Liebman. OES contract 14-16-0008-965 provided the page charges for publication. The scanning electron microscope photographs of radulae and jaws were taken by the author with a Cambridge S4-10 Stereoscan provided to the Field Museum of Natural History by NSF Grant BMS72-02149 A01. The SEM prints were prepared by Fred Huysmans. I am indebted also to Leslie Hubricht for loaning material of *Triodopsis platysayoides,* to Katy Baker for help with literature compilations, and to Jayne Freshour for aid with manuscript preparation. The OES staff, particularly Marc Imlay, has been most helpful and encouraging in these efforts.

STATUS OF KNOWLEDGE

Explorations for land snails in Missouri, Arkansas and what is now Oklahoma were carried out by James Ferriss in 1900 and 1901, and then by Henry A. Pilsbry and Ferriss in 1903. The papers by Pilsbry (1903) and Pilsbry and Ferriss (1907) contain data that is still essential for any field work in this region, although their major findings were summarized by Pilsbry (1940) in his monograph of the Polygyridae. This work, which synthesizes the efforts of a century, remains the basic reference for work on the family. Subsequent faunistic and descriptive papers by Leslie Hubricht, B. Branson, L. Lutz and others have provided additional distributional records. The conchological review of *Triodopsis* by Vagvolgyi (1968), and the review of the *T. fallax* group by Wayne Grimm (1975) contain much useful information.

Potentially the most significant studies are those of Glenn R. Webb (1952, 1954a, 1954b, 1959, 1961, 1974) on mating behavior and anatomy. Unfortunately these papers are difficult to use. Webb's supraspecific taxa were ignored by Vagvolgyi (1968) and Grimm (1975). The subgeneric and sectional names *Wilcoxorbis* (Webb, 1952), *Aphalogona* and *Ragsdaleorbis* (Webb, 1954b), *Haroldorbis* and *Shelfordorbis* (Webb, 1959), and the subfamily Ashmunellinae (Webb, 1954a) are validly proposed taxa and must be included in any revision of polygyrid classification.

The characters that have been used to define supraspecific categories are few in number. Mostly they involve alternative states, such as: penis sheath and retentor muscle (present or absent); epiphallus (present, absent or vestigial); duct of spermatheca (slender or swollen); verge (present or absent); number of major pilasters inside the penis (one or two); and the size of

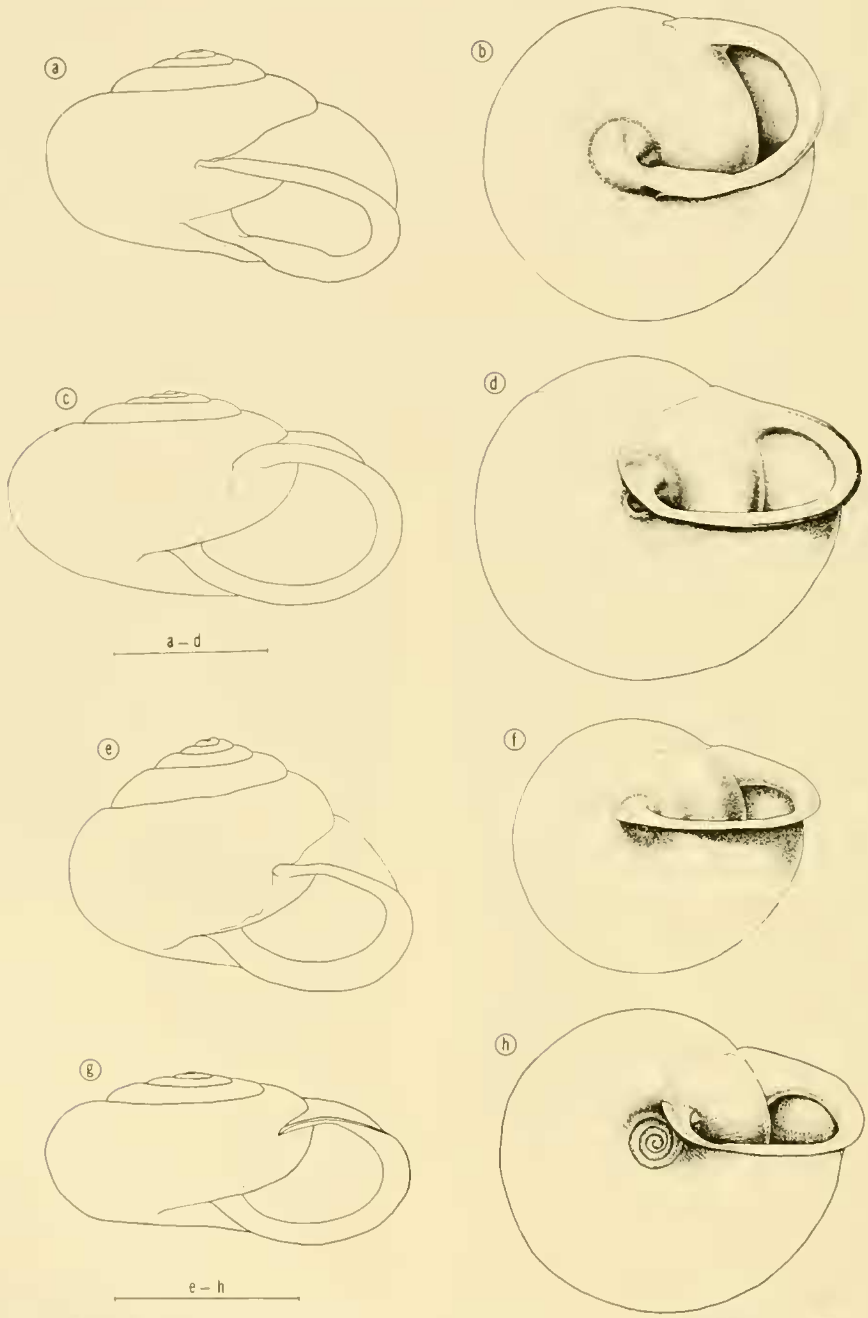


FIG. 1. *Shells of Ozarkian Polygyridae:* **a-b**, Triodopsis albolabris alleni *(Wetherby). FMNH 176127, Tenkiller State Park, Sequoyah Co., Oklahoma;* **c-d**, Mesodon binneyanus *(Pilsbry). FMNH 176008, Rich Mt., Polk Co., Arkansas;* **e-f**, Mesodon clausus *(Say). FMNH 176220, Calico Rock, Izard Co., Arkansas;* **g-h**, Mesodon clenchi *(Rehder). FMNH 176059, Mt. Nebo State Park, Yell Co., Arkansas. Scale lines equal 10 mm.*

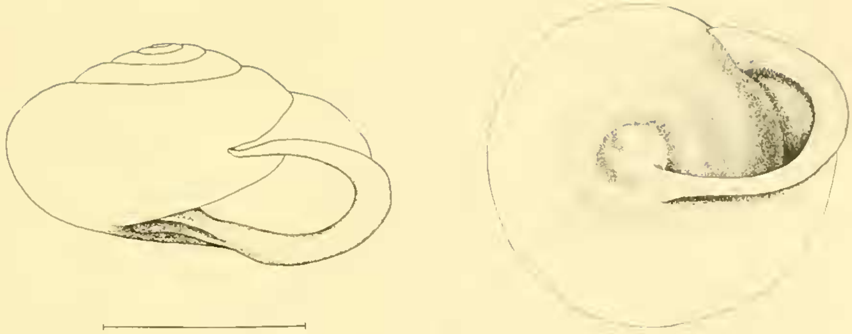


FIG. 2. *Shell of* Triodopsis divesta *(Gould). FMNH 176082, Magazine Mt., Logan Co., Arkansas. Scale line equals 10 mm.*

the papillae in the upper chamber of the penis. Although Pilsbry (1940: 703) had pointed out that the finer structure inside the penis should be investigated, subsequent workers have ignored this suggestion.

Triodopsis platysayoides and *Mesodon clenchi* (Rehder, 1932) had not been dissected previously, and only fragmentary data had been published concerning the structures of *Triodopsis divesta* and *Mesodon clausus* (Say, 1821). New details on the structures of *Mesodon binneyanus* (Pilsbry, 1899) and *Triodopsis albolabris alleni* are presented.

SHELL CHARACTERS

The absence of any major shell differences between species of *Mesodon, Triodopsis,* and *Allogona* that lack apertural barriers has confused students and collectors of the group for more than a century. Particularly in the Ozarkian region, several *Mesodon* and *Triodopsis* are conchologically quite similar. They have differences in the lip and umbilical region, but most previous illustrations fail to show these features. New line drawings are presented here to demonstrate such distinguishing characters.

Triodopsis (Neohelix) albolabris alleni (Wetherby) is highly variable in size and color, ranging as adults from 17-32 mm. in diameter. The relatively depressed spire, fairly sharp descension of the body whorl just before the aperture (fig. 1 *a*), presence of a thickened ridge on the basal lip (figs. 1 *a, b*), and sharply defined union of the columellar region to the umbilical covering (fig. 1 *b*) present a distinct contrast to the *Mesodon* (figs. 1 *c-h*). *Triodopsis (Neohelix) divesta* (Gould) generally is much smaller in size, mostly 17-21 mm. in diameter, has a distinctly weaker ridge on the basal lip (fig. 2 left), shows only slight descension of the body whorl near the lip, and has a very gradual merging of the columellar lip into the umbilical covering (fig. 2 right). Small specimens of *T. a. alleni* can be confused with normal *T. divesta*, but the differences outlined above are sufficient to enable identification.

Mesodon binneyanus (figs. 1 *c-d*) and *M. clenchi* (figs. 1 *g-h*) differ from each other most obviously in umbilical size, degree of lip reflection, and body whorl thickness, while *M. clausus* (figs. 1 *e-f*) has a higher spire, narrow lip, and a more angular insertion of the columellar lip (fig. 1 *f*). There is partial size overlap among these species. *M. clausus* (10-20 mm. in diameter) normally is smaller than *M. binneyanus* (16-28 mm.) and *M. clenchi* (19-23 mm.).

In many places three or more of the above species are sympatric, at least to the extent of living on the same slope or in the same ravine. A compilation of recorded localities in Arkansas, Oklahoma and Missouri for *T. divesta, T. a. alleni,* and *M. binneyanus*, for example, showed that for the 35 *T. divesta* localities, *T. a. alleni* also was recorded from 16 of these. Of the 23 localities known for *M. binneyanus, T. a. alleni* also has been taken at five, *T. divesta* at two, and at an additional two localities, all three species have been collected. The exact ecological relationships between these species are unknown, and a comparative ecological survey would be well worthwhile.

TERMINAL GENITALIA

The degree to which the terminal genitalia function in "species recognition" and the extent to which major differences in structures of this region make hybridization difficult or unlikely vary greatly from group to group of land snails. Webb (1952, 1954a, 1954b, 1959, 1961, 1974) has published voluminously on mating behavior and anatomies of polygyrid snails, with the cited references only serving as a locator for his studies. Grimm (1975) reported evidence of hybridization in the field and many laboratory crossings among *Triodopsis, s. s.* The situation in polygyrids is quite complex. All this report can do is to focus on some structural features for future investigation and to report on some previously undissected species.

Rather than present formal descriptions, comments are restricted to comparisons between structures in order to emphasize features with potential phylogenetic significance and of use in classification.

The classic key difference between *Mesodon* and *Triodopsis* involves the presence in the latter of a penis sheath (PS) and a continuation of the penial retractor muscle (PR) from its insertion on the vas deferens (VD) or penis (P) apex to the penis sheath. This continuation sometimes is called the "penis retentor muscle". The length of the sheath varies greatly, being long in *T. platysayoides* (fig. 3 *b*), short in *T. divesta* (fig. 4 *b*), and intermediate in *T. a. alleni* (fig. 5 *a*). These differences were constant in the materials examined. The sheath in *T. platysayoides* (fig. 3 *b*) also has a very unusual muscle attachment, in that it essentially spreads completely around the penis and onto the inside of the sheath, whereas in the other species it fastens to one portion of the sheath wall (fig. 4 *b*). All *Triodopsis* dissected to date agree in having two sections to the penis. The upper chamber has one very large pilaster plus a large microsculpture of papillae, while the lower chamber, the area below the apex of the penis sheath, has a series of simple longitudinal pilasters (PP) that continue into the atrium (Y). The relative length of the two chambers varies from species to species (compare figs. 3, 4, 5) and the lower chamber sometimes shows a distinct difference in pilaster size below the penis sheath when compared with the area of the penis sheath (compare figs. 3 *b*, 4 *b*).

There are obvious and major differences in the size and spacing of the papillae in the upper penis chamber (see figs. 3, 4 and 5). What has not been recorded previously, is the variation in apical penis structures. Although *Xolotrema* and *Neohelix* were reported to have verges (Webb, 1952), any differences in verge size and form were not recorded or illustrated. In *T. platysayoides* (fig. 3 *b*) there is no trace of a verge, while in *T. a. alleni* (fig. 5 *a*) the verge

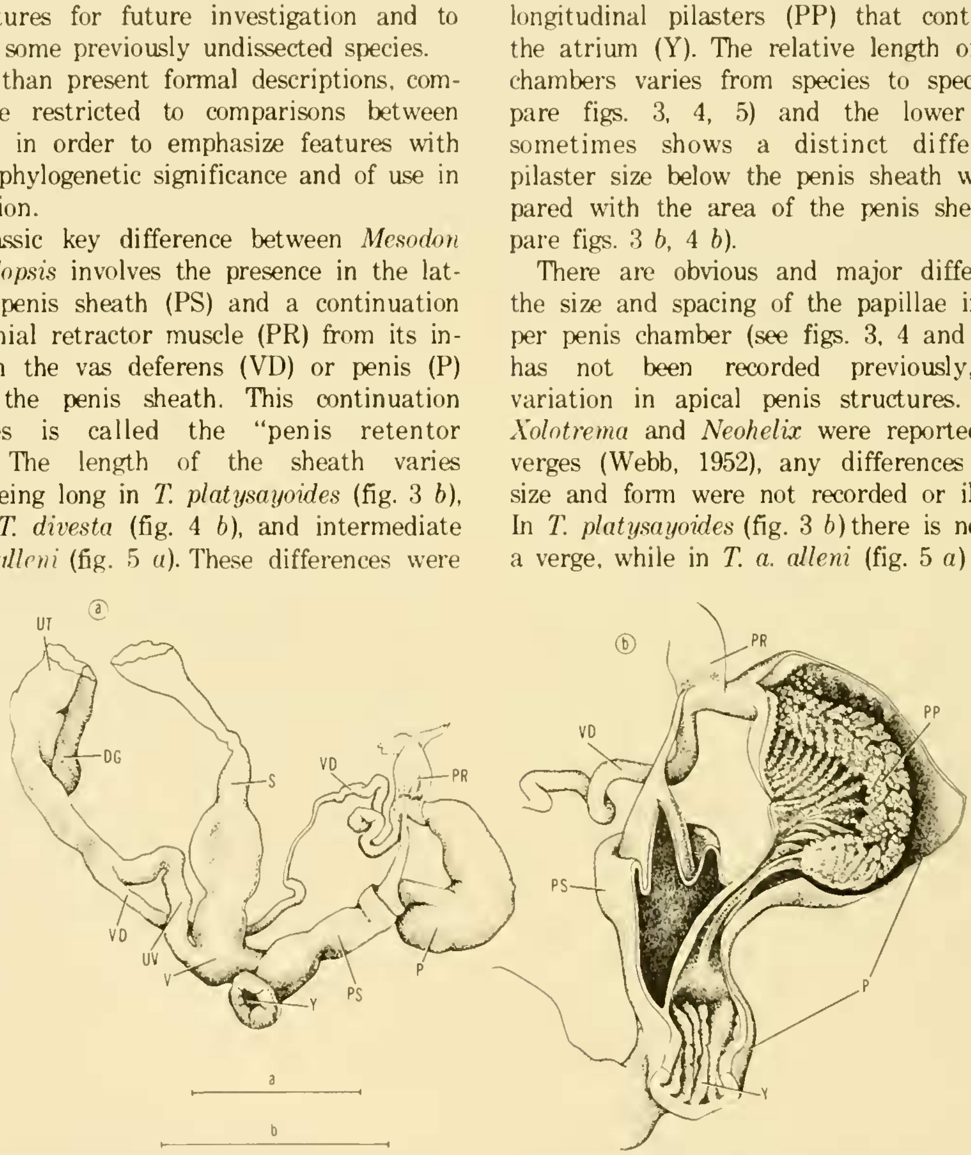


FIG. 3. *Genitalia of* Triodopsis (T.) platysayoides *(Brooks). Cooper's Rock, Monogalia Co., West Virginia. Leslie Hubricht 11860:* **a**, *terminal genitalia;* **b**, *interior of penis and penis sheath. Scale lines equal 5 mm.*

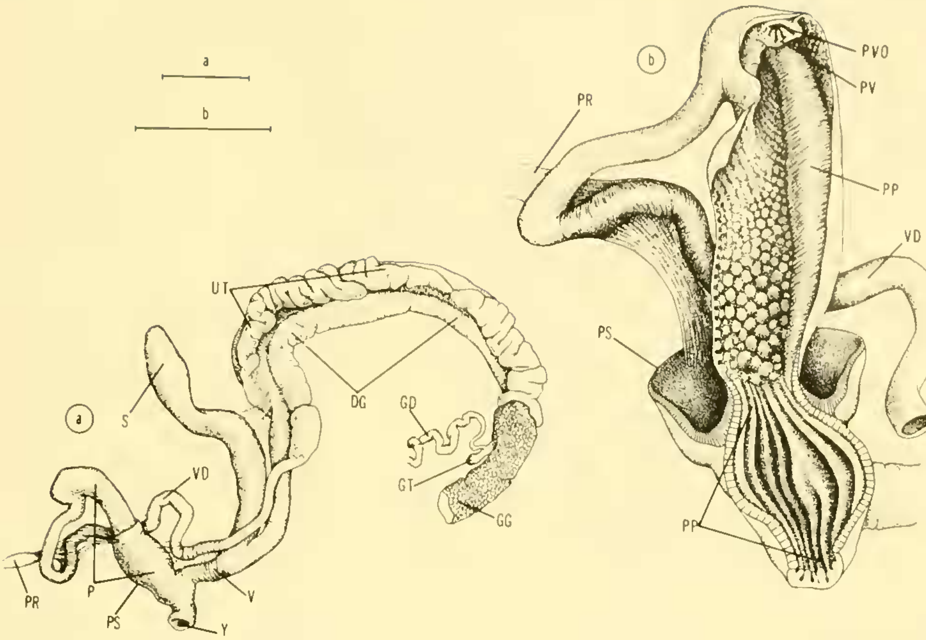


FIG. 4. *Genitalia of* Triodopsis (Neohelix) divesta *(Gould). FMNH 176082, Magazine Mt., Logan Co., Arkansas;* **a,** *terminal genitalia;* **b,** *interior of penis and penis sheath. Scale lines equal 5 mm.*

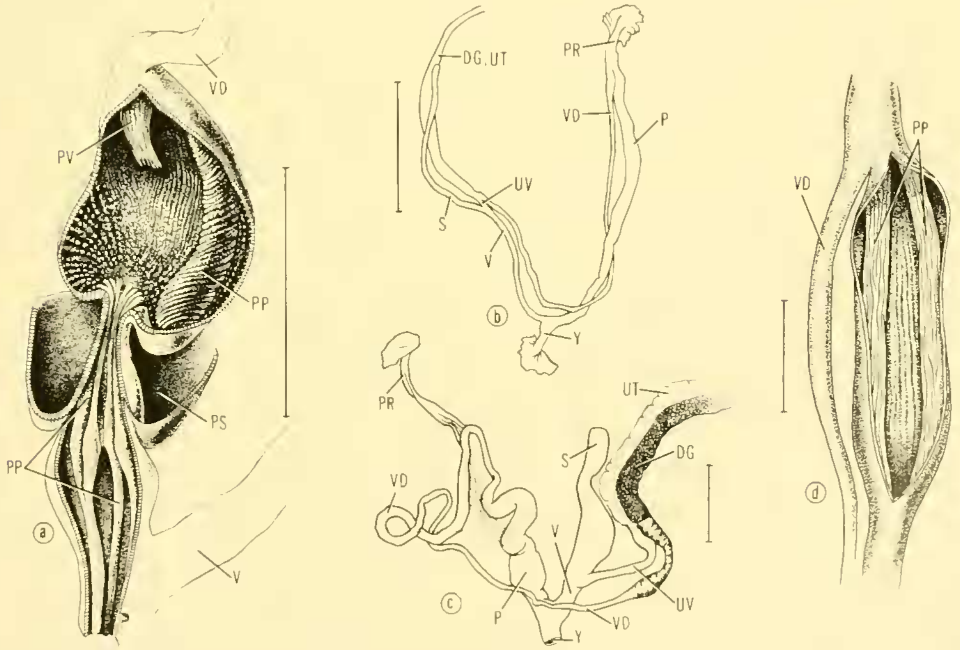


FIG. 5. *Genitalia of* Triodopsis (Neohelix) albolabris alleni *(Wetherby) and* Mesodon (M.) clenchi *(Rehder):* **a, c,** T. (N.) a. alleni. *FMNH 176127, Tenkiller State Park, Sequoyah Co., Oklahoma.* **a,** *interior of penis;* **c,** *terminal genitalia;* **b, d,** M. (M.) clenchi *(Rehder). FMNH 176059. Mt. Nebo State Park, Yell Co., Arkansas;* **b,** *juvenile terminal genitalia;* **d,** *interior of apical penis region. Scale lines for* **a-c** *equal 5 mm., scale line for* **d** *equals 1 mm.*

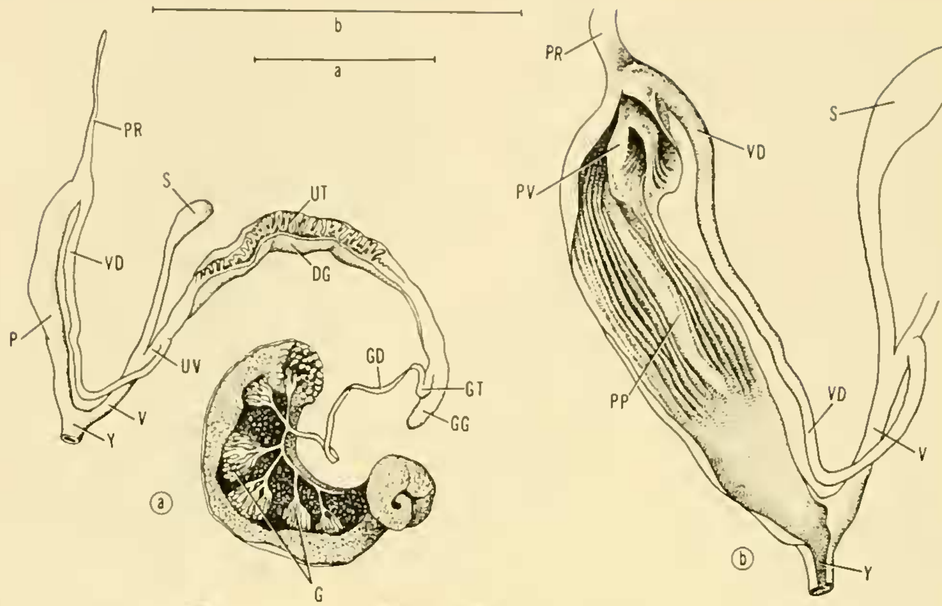


FIG. 6. *Genitalia of* Mesodon (M.) clausus *(Say). FMNH 176220. Calico Rock, Izard Co., Arkansas:* a, *genitalia;* b, *interior of penis. Scale lines equal 5 mm.*

(PV) is a very large, conical structure with terminal pore. In the often sympatric *T. divesta* (fig. 4 *b*), the verge is a flap-like opening to one side of the slightly recurved main pilaster and the pore (PVO) is quite large. The differences in chamber lengths, papillae size and number, and verges between *T. a. alleni* and *T. divesta* probably are sufficient to prevent hybridization.

Equally significant variations can be found in species of *Mesodon*. *M. clausus* (fig. 6 *b*) has a vergic papilla through which the vas deferens opens and only a single elevated pilaster (P); *M. clenchi* (fig. 5 *d*) has two pilasters of equal size and apparently no vergic papilla; and *M. binneyanus* (fig. 7 *e*) has two unequal pilasters that join apically into a flap-like arrangement, but with the vas deferens entering through a simple pore (DP) above the pilaster junction. A talon (GT) is well developed in *M. binneyanus* (fig. 7 *b*), but is only a reflexed area in *M. clausus* (fig. 6 *a*), without being differentiated from the hermaphroditic duct (GD). All examined *Mesodon* had a relatively long vagina (V), short free oviduct (UV), spermatheca (S) with slender shaft, finger-like albumen gland (GG) and showed no unusual features in the prostate (DG) and uterus (UT). The ovotestis (G) of *M. clausus* (fig. 6 *a*) is illustrated, but most other taxa had this organ in a reduced stage and it was not studied.

Mesodon binneyanus (fig. 7) has a very large penis that is substantially longer than the shell diameter. Pilsbry (1940: 740, fig. 445, D) used cross-sections of the penis to establish basic structures. The more detailed drawings presented here provide further details of structure. The apical portion (fig. 7 *e*) has a short, lower, second pilaster that gradually merges into the penis wall. The main pilaster is very high, thin, and apically forms a flap-like stimulator. In mid-penis (fig. 7 *c*) the main pilaster is reduced in height, thicker, and there are no obvious subsidiary structures on the penis wall. In the basal section (fig. 7 *d*) the main pilaster is almost circular in shape, becoming flatly ovoid at the atrium, and there is a complex set of minor pilasters on the penis wall. Unlike the situation in *M. clausus* (fig. 6 *b*) there is no pilaster-free basal area to the penis.

JAW AND RADULAR STRUCTURE

A strongly ridged jaw with denticulated lower margin is characteristic of the Polygyridae. No study of jaw variation in ribbing or microstructure has been published. References to the jaw usually are restricted to

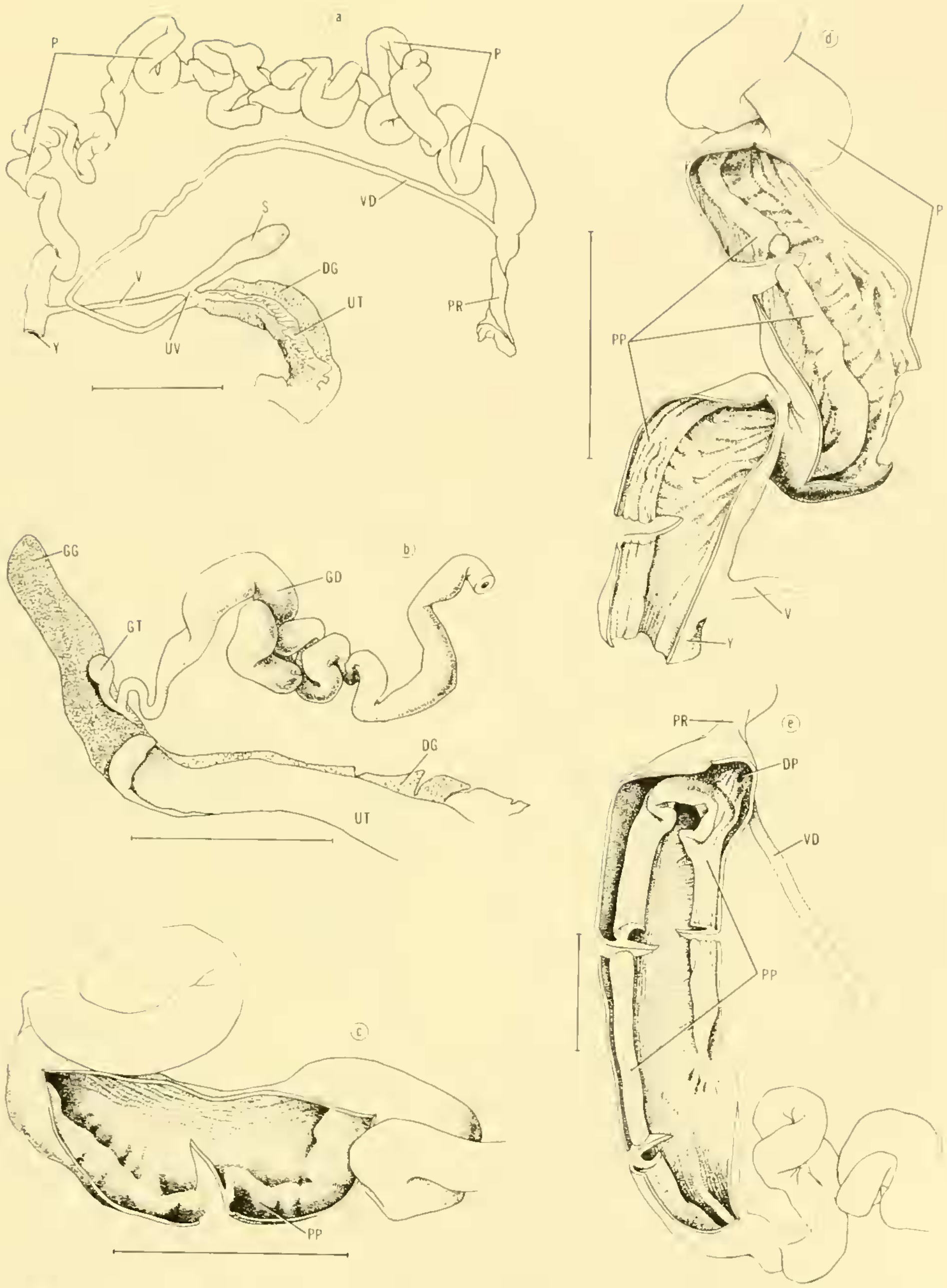
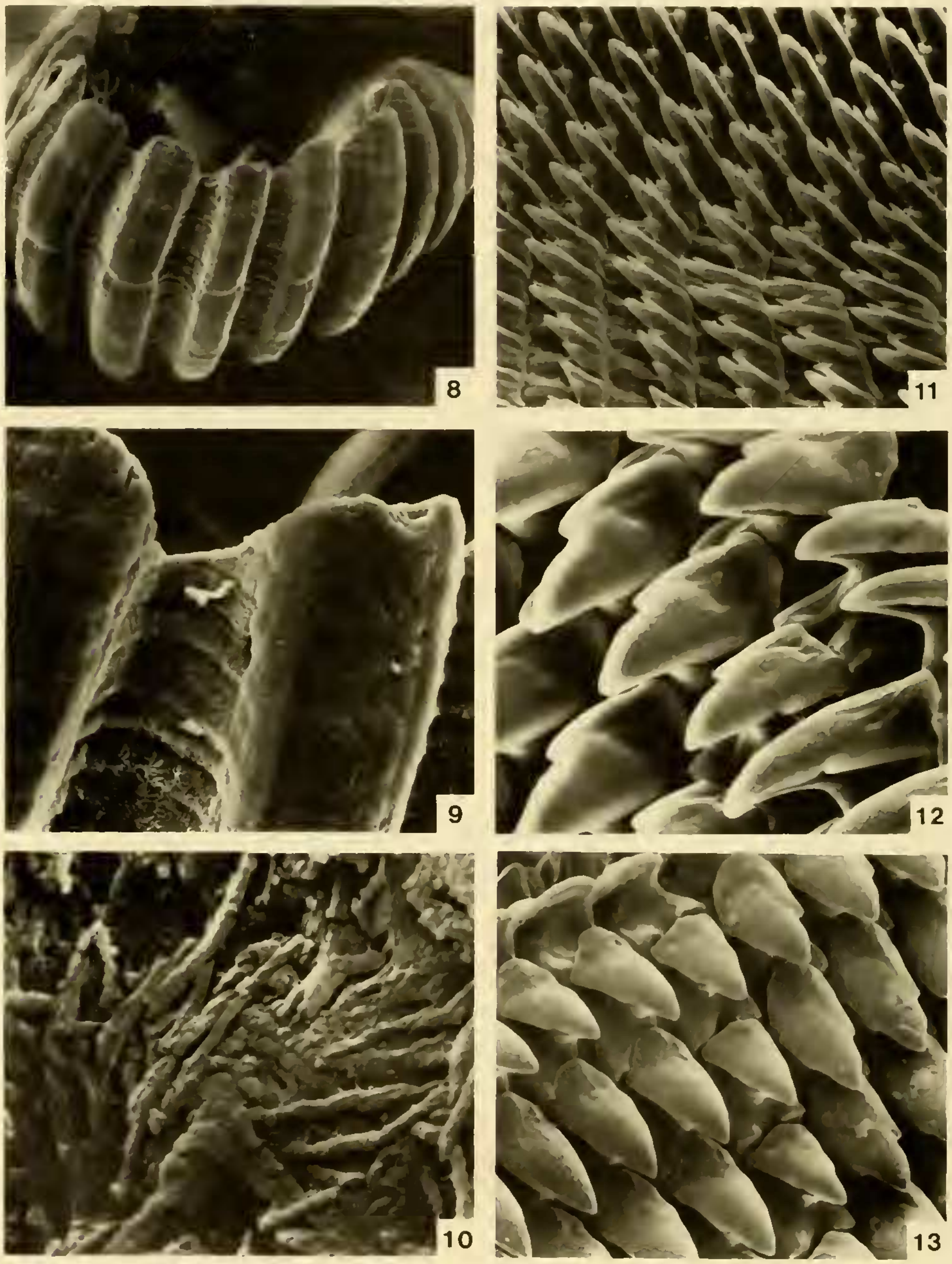


FIG. 7. *Genitalia of* Mesodon (M.) binneyanus *(Pilsbry). FMNH 176008, Rich Mt., Polk Co., Arkansas:* **a**, *terminal genitalia;* **b**, *apical genitalia exclusive of ovotestis;* **c**, *interior of mid-penis region;* **d**, *interior of basal portion of penis;* **e**, *interior of penis apex. Scale lines equal 5 mm. for* **b-e** *and 10 mm. for* **a**.

a few outline sketches indicating rib numbers (see Pilsbry, 1940: 912, fig. 522). The jaw of *Triodopsis albolabris alleni* (figs. 8-10) is illustrated here to show the typical shape (fig. 8), to demonstrate the wear surfaces on the denticulated lower margin (fig. 9), and to indicate that the jaw structure is fibrous in nature (fig. 10). Examples of the other species studied showed no significant differences. Indeed, the jaw microstructure is very similar to that of the helminthoglyptid *Humboldtiana fullingtoni* Cheatum, 1972 from Texas (see

Solem, 1974: figs. 3-5). Both series of photographs clearly show the horizontal incremental pattern of jaw growth and demonstrate the interlocking, basically vertical orientation of the microfibers.

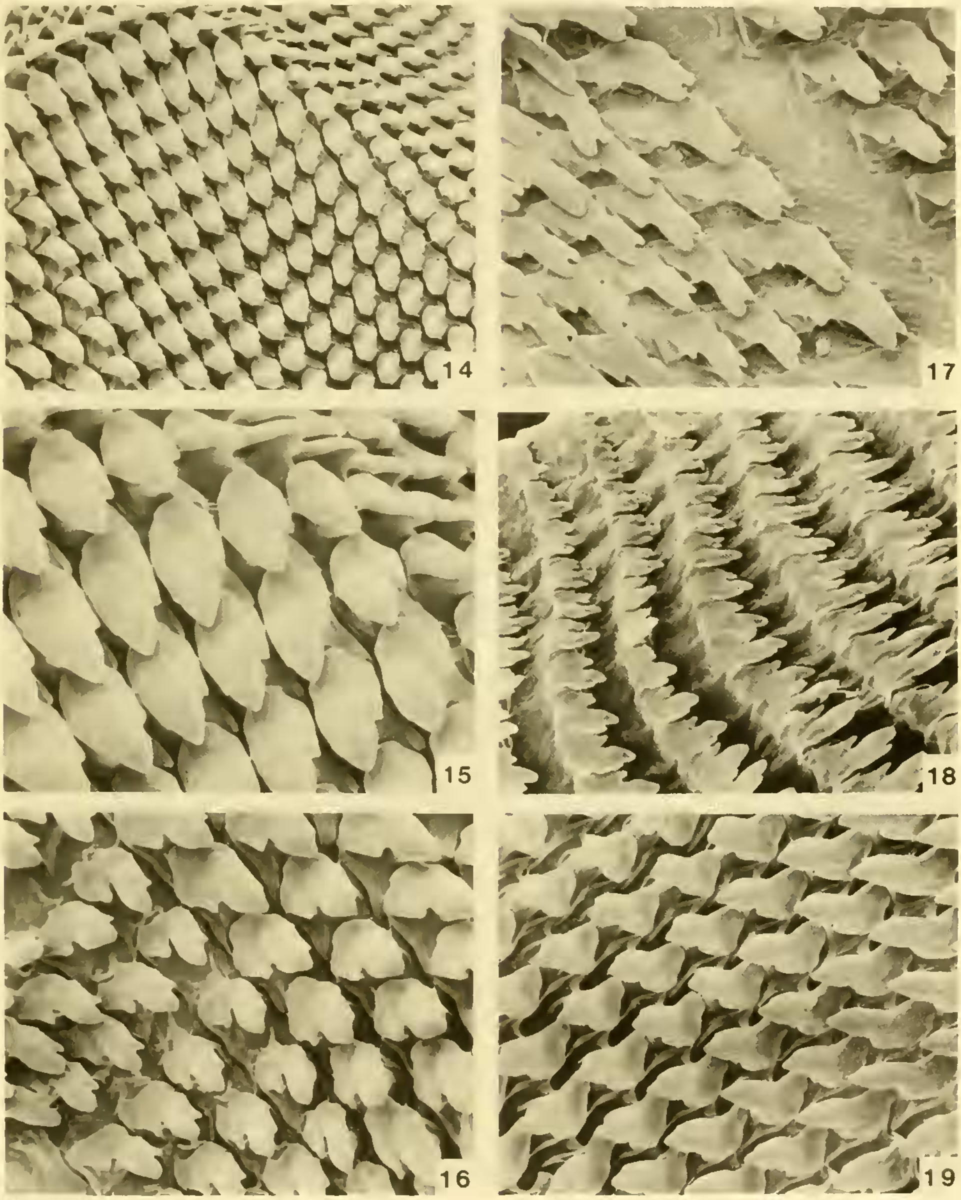
Radular data on polygyrids is equally



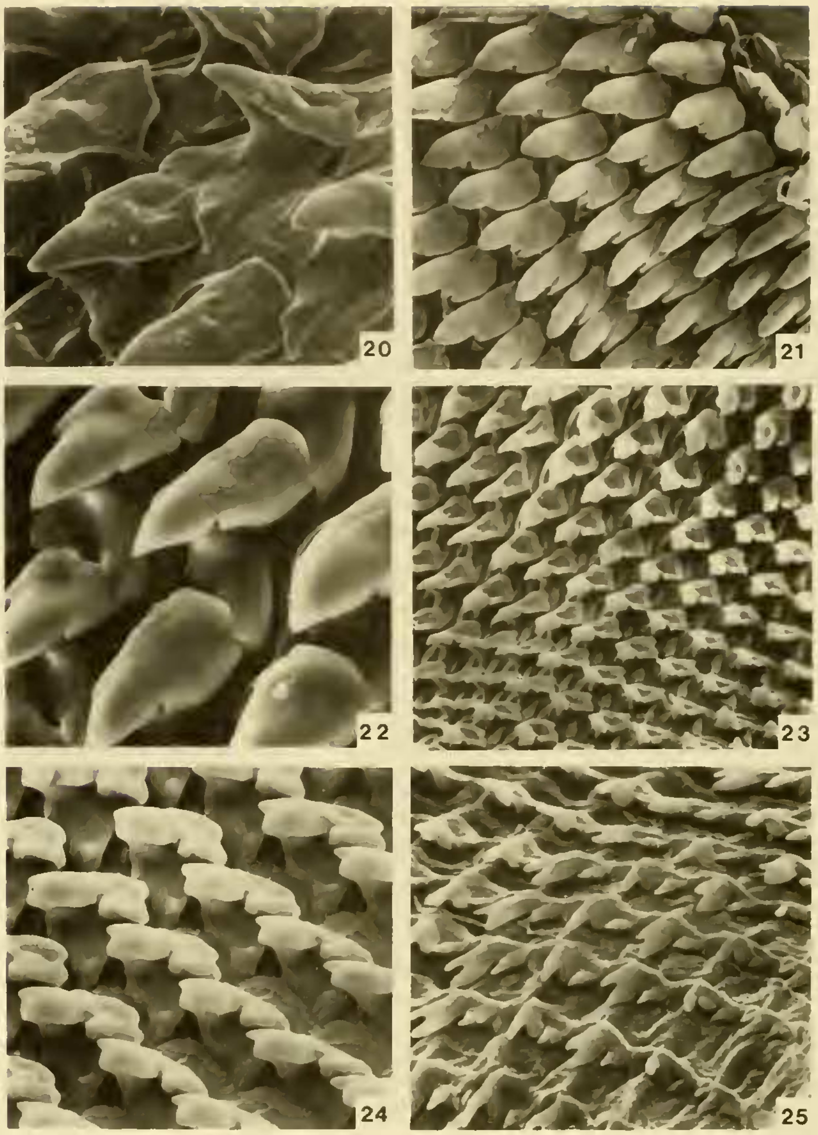
FIGS. 8-13. *Jaw and radular teeth.* Figs. **8-10.** *Jaw of* Triodopsis (Neohelix) albolabris alleni (Wetherby). *FMNH 176127.* Fig. **8.** *Entire jaw, lower margin at top of figure. 92×.* Fig. **9.** *Detail of two ridges on lower margin and inter-ridge area. 375×.* Fig. **10.** *Fibrous area between two ridges shown in Fig. 9, greatly enlarged. 5,725×.* Figs. **11-12.** *Radular teeth of* T. (N.) a. alleni *(Wetherby). FMNH 176127.* Fig. **11.** *Transition zone between lateral (upper) and marginal (lower) teeth near posterior end of radula. 370×.* Fig. **12.** *Central (tricuspid) and early lateral teeth. 625×.* Fig. **13.** *Central and early lateral teeth of* Triodopsis (T.) platysayoides *(Brooks). Leslie Hubricht 11860. 350×.*

meager. Pilsbry (1940: 703) summarized reported variation in *Mesodon*, where several species apparently lack ectocones. I suspect that this is partly individual variation and partly results from the deficiencies of optical viewing. *Mesodon clausus*, for example, is supposed to lack ectocones on all but the outermost marginals, yet traces can be seen (figs. 26-27) on the first laterals and there are prominent ectocones on the outer teeth (figs. 28-29). *M. clausus* does differ in having the cusps on the outer marginals serrated (fig. 29), but even this may be subject to individual variation.

The prominence of the side cusps on the rachidian (central) tooth vary from the large and conspicuous ones found in *M. clenchi* (up-

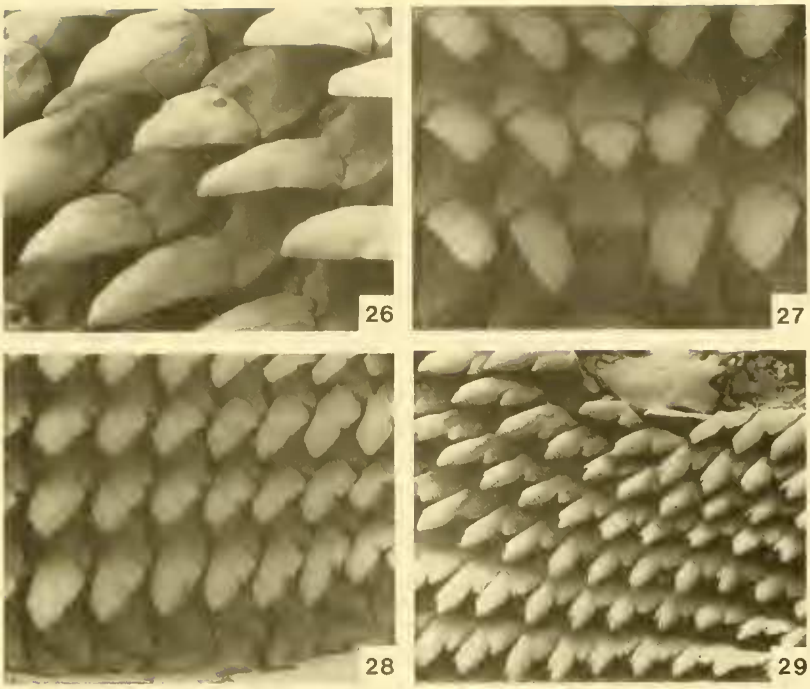


FIGS. 14-19. *Radular teeth.* Figs. **14-17.** Triodopsis (T.) platysayoides *(Brooks). Leslie Hubricht 11860.* Fig. **14.** *Part row of teeth, not including outer marginals. 140×.* Fig. **15.** *Transition zone between laterals and marginals. 345×.* Fig. **16.** *Outer marginals. 355×.* Fig. **17.** *Outermost marginals. 355×.* Figs. **18-19.** Mesodon (M.) binneyanus *(Pilsbry). FMNH 176008.* Fig. **18.** *Outermost marginals. 332×.* Fig. **19.** *Transition between laterals and marginals. 342×.*



FIGS. 20-25. *Radular teeth.* Figs. **20-21.** Mesodon (M.) binneyanus *(Pilsbry). FMNH 176008.* Fig. **20.** *Central and 1st lateral teeth. 670×.* Fig. **21.** *Transitional between lateral (upper left) and marginal (lower right) teeth. 395×.* Figs. **22-25.** Mesodon (M.) clenchi *(Rehder). FMNH 176059.* Fig. **22.** *Central and early lateral teeth. 762×.* Fig. **23.** *Transition between lateral (left) and marginal (right) teeth. 305×.* Fig. **24.** *Transitional change in basal plate structure between laterals (left) and marginals (right). 535×.* Fig. **25.** *Outermost marginal teeth. 600×.*

per left of fig. 22) and *Triodopsis albolabris alleni* (fig. 12), to a total absence in *T. platysayoides* (fig. 13). *M. clausus* (fig. 26) and *M. binneyanus* (fig. 20) are intermediate in cusp prominence. Ectoconal size on the early lateral teeth correlates with the side cusp prominence on the central tooth. If the central tooth has prominent side cusps, the laterals have a prominent ectocone, and small cusps occur on both at the opposite extreme (see figs. 12, 13, 20, 22, 26). These same illustrations show that the pattern of interrow tooth support for the central and early lateral teeth is nearly identical. The anterior flare on a lateral tooth under stress fit neatly into a groove on the outer side of the basal plate on the next anterior lateral tooth (see figs. 12, 13, 20, 22, 26, 27). The central tooth has a raised buttress on each



FIGS. 26-29. *Radular teeth of* Mesodon clausus *(Say). FM-NH 176220.* Fig. **26.** *Central and first lateral teeth. 595×.* Fig. **27.** *Central and early lateral teeth seen from a low posterior viewing angle. 425×.* Fig. **28.** *Transition between lateral and marginal teeth. 335×.* Fig. **29.** *Mid-marginal and outer marginal teeth. 365×.*

side of the basal plate. Because of the angle at which these photographs were taken, the impression is given that the anterior flare of the lateral tooth is not or only slightly curved upwards. In fig. 23, the angle of view is such that the upward curve (see left side of photograph) of the anterior flare is more evident.

The change from lateral to marginal teeth involves a number of alterations. Fig. 11 shows clearly the higher angle of the cusps in the laterals (upper), with the change to a much lower angle in the marginals (lower) occurring in just a few teeth. Seen in more vertical view (figs. 14, 15, 19, 21, 23, 28), the coherent pattern of cusp change that involves narrowing and elongating the mesocone, an increase in ectoconal prominence, change in shape for the anterior flare, often (figs. 15, 28) a centerwards shift in angle for the mesocone, and appearance of a small endocone, is clearly demonstrated. The change in the basal plate, which involves shortening, first reduction and then loss of the support ridge, then gradual elimination of the anterior flare, is shown in figs. 24 and 28 particularly well because of the viewing angle (fig. 24) and partly torn radula (fig. 28).

The marginal teeth, particularly the outermost (figs. 17, 18, 23, 25, 29) ones, can become multicuspid, normally show endoconal development, and may become quite shortened and probably are almost without function in feeding. They are held parallel to the basal membrane, which is quite in contrast to the high elevation of lateral teeth (figs. 11, 20).

In terms of basic structure and pattern of functioning, the radulae examined here show no major differences between species, much less between genera. The different angles of view do permit interpreting functional aspects. Several species have been illustrated to emphasize their essential similarity.

DISCUSSION

Particularly within *Triodopsis,* the variation in verges, papillae of the upper penis chamber, penis sheath length and muscle attachment, present characters potentially of high value in assessing relationships. Radular cusp variation is greater within *Mesodon* and *Triodopsis* than between the two genera. Shell differences between the sympatric taxa involve growth patterns and columellar-umbilical region structures.

Triodopsis platysayoides is a rare and potentially endangered species, but *Mesodon clenchi* was found to be more widely distributed than had been suspected and it seems in no danger of extinction at the present time. The other species discussed here have wide distributions and may be considered common at the present time.

Because the barrier-free *Mesodon* and *Triodopsis* of Missouri, Arkansas and Oklahoma are widely distributed, frequently sympatric, usually highly variable in size and color, they present excellent potential for studies of ecological differences under sympatry and for variational analysis.

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TREMATODE PARASITISM IN THE SPHAERIIDIDAE CLAMS, AND THE EFFECTS IN THREE OTTAWA RIVER SPECIES

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ABSTRACT

There is a seasonal occurrence of rediae of the trematode, Crepidostomum cooperi *Hopkins, in the digestive gland of* Musculium securis *(Prime) in Britannia Bay of the Ottawa River near Ottawa, Canada. Growth and longevity of infected clams do not appear to be affected but reproduction is usually inhibited. Similar effects seem to occur in parasitized specimens of* Musculium transversum *(Say) and* Sphaerium striatinum *(Lamarck). A review of the incidence of trematode parasitism in Sphaeriidae is given.*

INTRODUCTION

While the incidence of trematode parasitism in Sphaeriidae is well documented (see Table 3), there is very little known on the effects of this parasitism. The purpose of this study is to examine the effects of trematode parasites on growth, longevity, and reproduction in *Musculium securis*, *Musculium transversum*, and *Sphaerium striatinum* that were collected seasonally from Britannia Bay in the Ottawa